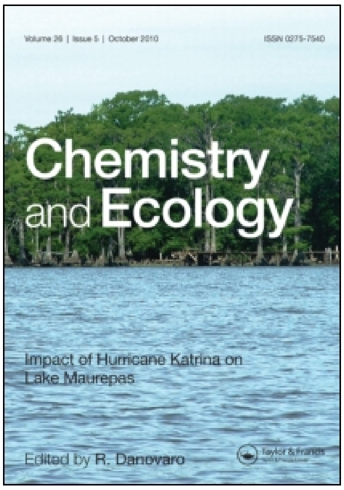

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Meiofauna of the Adriatic Sea: present knowledge and future perspectives

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Meiofauna of the Adriatic Sea: present knowledge and future perspectives

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Owing to technical problems and difficult taxonomic identification, meiofauna have been generally less studied than macrofauna. However, the role of meiofauna in marine ecosystem functioning, and their effective and rapid response to anthropogenic alterations and climatic changes have recently been acknowledged, leading to increasing scientific and applied interest. At present, systematic and biogeographic knowledge of the meiofauna of the Adriatic Sea is extremely heterogeneous, because most of the data are limited to a few taxa and the sampled areas are scattered, being located mainly in the coastal areas of the northern basin. Analysis of the composition and distribution of meiobenthic groups in the Adriatic Sea highlights the presence of several endemisms. Meiofauna also include bioindicator taxa, which allow assessment of the quality of marine sediments; this is particularly useful in systems characterised by the synergistic effect of different forms of anthropogenic impact, such as the Adriatic basin. Current knowledge about the ecology of the meiofauna and use of this component in applied ecological studies, along with the availability of a standardised protocol for the analysis of meiofaunal assemblages, allows us to recommend formal acknowledgement of the need to integrate information derived from the analysis of macrofauna with information derived from the study of meiofauna. Future research based on the simultaneous use of both of these benthic components will allow faster and more accurate evaluation of the response of coastal marine ecosystems to anthropogenic disturbance.

Keywords: meiofauna; Adriatic Sea; biodiversity; ecology; bioindicator; conservation

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1. Introduction

1.1. *Definition*

Meiobenthos (from ancient Greek *meio*, smaller) was originally defined as the benthic component intermediate in size between the macrobenthos and the microbenthos. The body size range of meiobenthic animals (meiofauna) is set by standardised sieve mesh sizes (1000 to 44 µm, in some cases down to 20 µm). However, meiofauna are much more than a mere size category: they also share a distinctive lifestyle, ecological relations and often evolutionary traits, and thus are seen as an ecological unit of metazoans, which also include large protozoans (foraminifers, ciliates).

1.2. *History of research on marine meiofauna*

Although most meiobenthic animals have been known since the invention of the microscope, and a great number of taxonomic reports and biological studies on single taxa go back to the mid-nineteenth century, research focusing strictly on the diversity and ecology of meiofauna is relatively recent. Important scientific contributions forming the basis of current knowledge were made by Remane [1]. He first developed methods for sampling the interstitial, epibenthic and periphytic micrometazoans and acknowledged the sand meiofauna as a true biocoenosis. Following Remane's activity and teaching, a number of other German researchers, Ax, Gerlach and Riemann among them, continued faunistic and ecological studies on meiofauna, and also improved collecting methods. In the 1930–1960s, meiobenthic research also began in Britain with Moore, McIntyre, Nicholls, Mare and Boaden, and in France with the studies by Swedmark on the Normandy coast and Delamare-Deboutteville along the Mediterranean shores. The development of meiobenthic research on the America continent dates from the 1940s with descriptions of new, important taxa like Mystacocarida and Cephalocarida (Crustacea), followed by the morphological and ecological studies by some European researchers working in the USA in the 1960–1980s, like Cobb, Riedl, Wieser and Rieger (see [2] for an exhaustive list of references). Since the 1970s, the impetus given by Coull and his school to the study of environmental constraints on the meiofauna and to the application of field experimental methods has led to increasing general interest in marine meiofauna. In Europe, the reference centres for research on meiofauna, and nematodes in particular, are nowadays represented by the University of Gent (Department of Marine Biology), the British Natural History Museum of London, and the Plymouth Marine Laboratory (UK). In Italy, studies on meiofauna started in the 1960s at the University of Bari, and are now carried on by several research groups (Universities of Ancona, Bari, Bologna, Genoa, Modena-Reggio Emilia, Naples, Sassari, Urbino).

1.3. *The Adriatic Sea*

The Adriatic Sea is an elongated, shallow basin of the central Mediterranean Sea, oriented in a NW–SE direction and characterised by the most extensive development of continental shelf in the Mediterranean. The bathymetric features allow us to recognise three regions. The northern region is very shallow and gradually slopes with an average depth of ~35 m. The basin extends to 270 m depth in the central part, reaching 1250 m in the southern region. The Adriatic Sea connects with the Mediterranean Sea through the Strait of Otranto with a sill at 750 m depth. The general circulation is cyclonic with a flow directed north-west along the eastern coast and a return flow directed south-east along the western coast. The mean circulation shows seasonal variability according to changing winds and thermal fluxes during the year. Local cyclonic gyres characterise the general circulation in the three regions: the southern sub-gyre tends to persist throughout the year, the middle sub-gyre is more pronounced in summer and autumn, and in the northern region a cyclonic gyre is evident during the autumn in front of the Po River mouth. In general, the Adriatic Sea is a low nutrient system, but it is notably enriched by the input of nutrients, organic matter and clay from the Po River and a number of smaller Apennine rivers. Once the run-off products are introduced into marine ecosystems, their distribution is mainly determined by the pattern of the surface circulation. The nutrient load of fresh waters has greatly increased over the last decades showing an anthropogenic burden of chemicals on the Adriatic which may also include heavy metals. The middle and southern regions of the Adriatic Sea are characterised by a lower primary productivity, with poor continental inputs and benthic–pelagic interactions, except for the western coast, to which nutrient come from the northern basin by the southward coastal current [3].

2. Biodiversity and ecology of the marine meiofauna

2.1. *Ecological and geographical distribution*

The geographic distribution of most meiofaunal taxa is assumed to be extremely wide or even cosmopolitan. Taking into account the limited mobility of these animals, and the lack of pelagic stages, this distribution pattern appears enigmatic, and has been the object of great debate for several years. Mechanisms of passive dispersion may account for the wide distribution of many taxa, but recent molecular and ultrastructural research has revealed complexes of cryptic species, challenging current knowledge of the biogeography of meiofaunal taxa [4,5]. However, the refugial and selective interstitial habitat of the deep sea has allowed the survival of relict taxa and of highly specialised forms that, over time, tend towards isolation and sympatric speciation. The powerful genetic tools currently available may detect the scale and nature of similarities among different sites, as well as the possible ways and times of dispersion.

2.2. *Abundance and diversity*

Meiofauna represent the most abundant benthic group of metazoans in the marine bottoms, with abundances ranging, on average, from 10^5 to 10^6 individuals $\cdot$ m^{-2}, corresponding to a biomass of 1–2 g dw $\cdot$ m^{-2} in shallow waters [2]. Abundance and biomass values vary according to season, latitude, water depth, tidal exposure, grain size, habitat type, and other abiotic and biotic factors of the biotope. Highest abundances are typically measured in intertidal muddy estuarine habitats, whereas the lowest are typically encountered in the deep sea.

This little-known benthic group is more diverse than any other component of the marine biota: as many as 24 of the 35 animal phyla have meiobenthic representatives (Figure 1) that live in meiofauna all their life or for only a life phase. Three phyla have been found in the last 30 years, thus proving the high potential phyletic diversity of this benthic group. Nematodes are generally the most abundant taxon of metazoan meiofauna (often $>50\%$ of the total meiofaunal abundance, reaching a proportion of $>90\%$ in deep-sea sediments), with Copepoda Harpacticoida as a common co-dominant taxon. The other taxa are rarely present in significant abundance, more often with only few specimens. Among meiobenthic protozoans, Foraminifera are the most abundant in the marine realm and the most diverse group of shelled organisms in modern oceans.

2.3. *Adaptations and distribution in the habitat*

Because of the heterogeneity of the habitats colonised by meiofauna and the diversity of this benthic group, only a few morphological adaptations are shared by all meiobenthic animals,

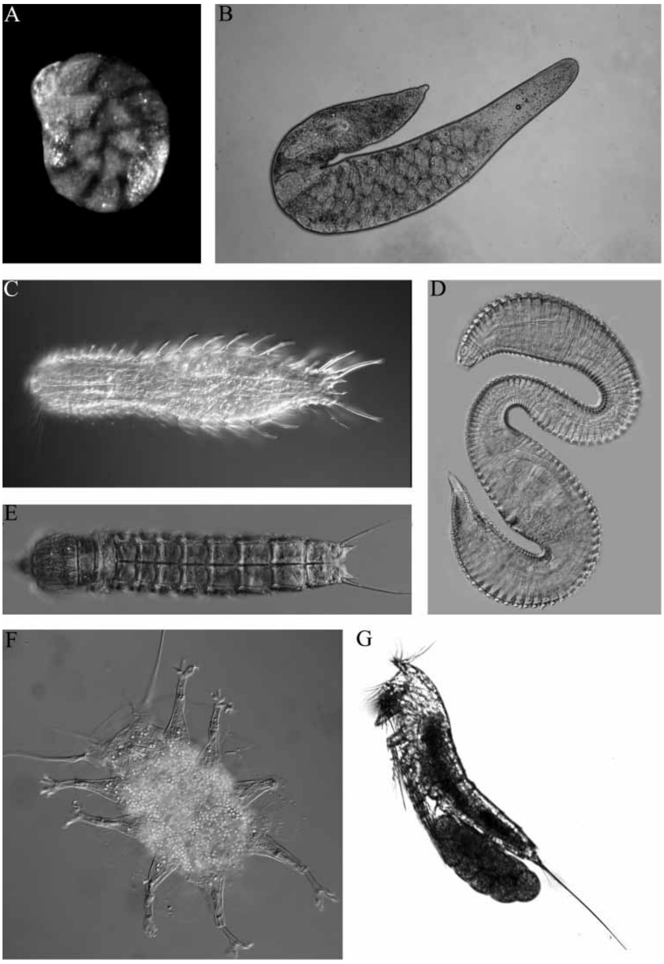

Figure 1. Representatives of the major meiofaunal taxa: (A) Foraminifera, (B) Proseriata (Platyhelminthes), (C) Gastrotricha Chaetonotida, (D) Nematoda, (E) Kinorhyncha, (F) Tardigrada, (G) Copepoda Harpacticoida.

and these especially apply to interstitial ones (*mesopsammon*). Living and moving through the narrow interstitial spaces of the sediment has allowed most interstitial animals, even those phylogenetically distant from each other, to evolve similar morpho-functional adaptations. Body miniaturisation up to dwarfism, and simplification of the body plan up to the loss of organs are common. A slender, thin and flexible body, and glandular or mechanical adhesive organs, often gathered in a long posterior tail, are essential for anchoring to sediment particles, especially in habitats subject to strong hydrodynamism. Stiffening of the body wall, often combined with secretion of adhesive mucus, favours the adhesion to the sediment, opposing the hydrodynamic stress. By contrast, fauna inhabiting muddy sediments do not conform to a particular morphology but are generally larger than interstitial fauna. Combined methods of locomotion have been realised by different meiofaunal taxa; body pigmentation and photoreceptors are generally reduced in meiofaunal forms, unlike the corresponding epibenthic ones, whereas static organs useful for orientation in the homogeneous, three-dimensional psammic system are widespread [2].

A number of physical, chemical and biotic factors concur in influencing habitat suitability for meiofauna. The shape, size and chemical composition of the sediment particles, and the water circulation appear to be of primary importance in conditioning the abundance and composition of the community. For example, the sediment grain size and structure play a key role in defining the porosity of the sediment and the surface available to prokaryotes, diatoms, microfungi and microalgae, which together are an important food item for meiofauna. Moreover, mucus and biofilms produced by these micro-organisms can decrease the erosive fluxes and the suspension of meiobenthic organisms due to near-bottom currents, thus stabilising the benthic environment and providing more reliable conditions for colonisation by meiofauna. Sediments with a median particle diameter $<125\,\mu m$ are especially colonised by burrowing taxa (e.g. Kinorhyncha), while the strictly interstitial meiofauna (e.g. Gastrotricha, Tardigrada) preferably live in sediments with grain size from 125 to $500\,\mu m$ [6].

The oxygen availability, pH, redox potential and hydrogen sulfide content are crucial in defining the vertical distribution of meiofauna. Most meiobenthic animals live in the upper few centimetres of the sediment as a consequence of the vertical gradient in oxygen concentration, which, in turn, is influenced by tidal fluxes or local alterations in habitat. Bioturbation caused by either macro- and meiofauna, and bioconstructions (e.g. tubes) locally modify the vertical gradient and produce a very complex three-dimensional network of oxygenated and sulfidic microniches, among which each meiobenthic taxon can find the most suitable microhabitat [7]. Activities of all benthic faunal groups may also lead to attraction (reproductive activities, bioturbation) or avoidance (disturbance, predation, competitive interactions) reactions that can modify the overall structure of the meiobenthic community. Ultimately, the balance between the quantity and food availability of organic matter is also a major factor determining the vertical distribution of most meiobenthic taxa.

The differentiated localisation of trophic sources can indeed be a primary factor which structures the horizontal distribution of meiofauna. The network of interactions between abiotic and biotic factors potentially controlling meiobenthic fauna is very complex, and their response to changes in these factors is dependent upon the spatial scale at which they occur. The presence and small-scale distribution of meiofauna appear to be mostly influenced by biotic variables, whereas their large-scale distribution seems to be rather related to abiotic factors.

2.4. *The role of meiofauna in marine benthic food webs*

Most meiobenthic organisms are deposit feeders, but numerous also are diatom-grazers and, particularly in deep-sea environments, bacterivores. Among the most abundant taxa are nematodes: the morphology of their mouth shape and size allows identification of their main food items, which permits easy classification of nematodes into trophic guilds, that, in turn, are used to investigate trophic and functional diversity. In this regard, nematodes can be divided into four trophic groups on the basis of Wieser's classification [8]: selective deposit feeders (or bacterivores; group 1A), which feed mostly on prokaryotes; nonselective deposit feeders (group 1B), feeding on organic detritus; epistrate-feeders (group 2A), feeding on benthic diatoms; and predators–scavengers–omnivores (group 2B), which can prey upon other meiofauna and macrofaunal juveniles. Recently Moens and Vincx [9] divided trophic group 1A into nematodes ciliate-feeders and bacterivores, and group 2B into obligatory and facultative predators. Harpacticoid copepods, the second main component of meiofauna, seem to have a significant microphytobenthos-based diet (mainly diatoms) whereas platyhelminthes are known to prey upon other meiofauna [10].

Meiofauna can enhance prokaryotic biomass by: (1) stimulating growth with excreted N- and P-rich dissolved metabolites; (2) secreting mucus threads colonised by micro-organisms which are, in turn, cropped by meiofauna (bacterial gardening); (3) sediment bioturbation activity which enhances oxygen diffusion rates stimulating aerobic prokaryotes; and (4) mechanical breakdown of detrital particles favouring prokaryotic decomposition. Estimates [11] report that 3% of bacterial biomass and 1% of diatom biomass can be removed hourly by meiofauna which consume the equivalent of their weight in microbial biomass every day.

Meiofauna are usually considered to be closely integrated into a ‘detrital trophic complex’ [12] but they also have various connections with other faunal compartments of the benthic system. First meiofauna, together with microfauna (protozoans), microphytobenthos, prokaryotes and detritus, are part of the ‘small food web’ within which they play a significant role. Second, meiofauna show numerous ties to the macrobenthos, occupying a pivotal position in the whole benthic food web not so much in terms of biomass, which is obviously low, but in terms of contribution to energy flow thanks to their higher turnover rate which yields high production levels. In fact, the small size is indeed coupled with a high metabolic activity and a rapid turnover (i.e. as the ratio of production to biomass, P:B), which is on average fivefold that of macrofauna, leading to similar production values even in systems dominated, in terms of biomass, by macrofauna. The meiofaunal P:B is, however, taxon specific and can vary from species to species within the same taxon. Therefore, it is difficult to assign a single value that could be generally valid, but a value from 9 to 10 is most commonly assigned [7].

Meiofauna play also an ecological role of primary importance within the benthic domain because they represent the link between organic detritus and higher trophic levels [13–17]. In sandy sediments, the interstitial lifestyle of most meiofauna avoids being preyed upon by macrobenthic organisms. So the production of meiofaunal organisms is rarely spread to higher macrobenthic trophic levels and represents a dead end in the food web. By contrast, in muddy sediments, meiofauna live mostly in the superficial layers, and thus are intensively exposed to predation pressure by several small macrobenthic animals such as small shrimps, crabs, polychaetes, ophiuroids and juvenile fishes (e.g. Gobidae, *Leiostomus*) [18–20].

There is also a reciprocal negative interaction between meio- and macrobenthos because of the life-trait peculiarities of the early life stages of several macrobenthic species. Indeed, many of the latter develop small planktonic larvae which, after settling, become elements of the so-called ‘temporary meiofauna’. Thus, if adult macrofauna feed on permanent meiofauna, the latter, in turn, can prey directly on the meiofauna-sized early stages of macrofauna leading to a considerable reduction in the macrobenthic offspring [12] and controlling the structure and composition of the adult macrobenthic assemblage (bottleneck hypothesis) [21]. Besides the merely trophic aspect, many other links mutually tie meio- and macrofauna in muddy sediments. Meiofauna break down macrofaunal faecal pellets, enhancing organic matter decomposition and bacterial growth rate for the benefit of the macrobenthic detritivore species. Moreover, bioturbation by infaunal macrobenthic species and oxygenation of reduced sediment by the activities of shrimps, clams and flatfishes may increase the production of meiofauna. Indeed, the role of meiofauna in the marine benthic systems seems to be much more complex than supposed and deserves to be investigated in order to understand the ecological importance of meiofauna in the benthic domain.

2.5. *Meiofauna diversity and ecosystem functioning*

The idea that biodiversity can significantly influence ecosystem function has been accepted even at societal levels. Results gathered from ∼20 years of investigations have generated evidence of the ecosystem consequences of biodiversity loss, but also several controversies on how diversity is related to, or affects, ecosystem functioning [18].

Oceans worldwide are experiencing impacts of unprecedented intensity and frequency, which are directly and indirectly causing alterations in the biodiversity, structure and organisation of marine assemblages. The hypothesis that a loss of biodiversity might threaten ecosystem functioning, thus reducing ecosystems’ goods and services, was postulated at the end of the 1990s

[22] and has recently been demonstrated for many marine ecosystems [23]. For example, at a local scale, the loss of marine biodiversity is particularly relevant along coastal oceans, where mangroves, coral reefs, seagrass beds and lagoons are progressively impacted [24–26]. Large pelagic predators (i.e. sharks, carangids and tunas) and their biodiversity are also at high risk because of overfishing [27,28].

Many field, manipulative and theoretical studies have identified positive saturating relationships between biodiversity and ecosystem functioning [27,29], but recent investigations carried out using nematodes as a model have allowed identifying positive nonsaturated relationships between biodiversity and ecosystem functioning of deep oceans worldwide [28]. Such a nonsaturated relationship, which predicts a major ecosystem collapse even with a minor loss of nematodes species richness, has been related to the occurrence of mutualistic and facilitative interactions among deep-sea species [29]. These studies highlighted the need to consider meiofauna in future studies aimed at addressing the role of biodiversity on ecosystem functioning.

2.6. *The use of meiofauna as a biological indicator*

The use of meiofauna as a biological indicator in marine biotopes is a relatively recent approach in the assessment and monitoring of ecosystem quality [30] that integrates standardised methods of studying macrofauna. The advantages of using meiofauna rather than macrofauna are numerous: ubiquitous presence, high number of species and individuals even in small samples, which make the statistical analysis reliable, high sensitivity of some taxa to pollution agents, rapid life cycle and thus rapid generation turnover, and low-cost sampling and handling. Some arguments traditionally advanced against this use of meiofauna underline the difficulties in identification, requiring microscopical observation and specialist expertise, the high sampling frequency necessary to compensate for the characteristic heterogeneous distribution of meiofauna, and, last but not least, the microscopic size of these animals which are not popular because they are not visible. However, new technologies and tools, like standardised bioassays for general use [31,32], electronic identification keys and new indices based on meiofauna [33], currently allow and promote the use of meiofauna in impact studies. Ecotoxicological studies based on a genetic approach are also increasing [34].

Nematodes and copepods are the taxa generally considered to be the most suitable for studying the ecological conditions of the meiofaunal community [6,35]. The divergent auto-ecological characters of the two taxa allowed Raffaelli and Mason [36] to propose the numerical ratio Nematoda/Copepoda as a useful index to check variations of the sediment ecosystem. Later this index was abandoned because it proved to be affected by many environmental factors, such as the horizontal distribution, sediment granulometry, seasonal variability and also pollution [37,38]. Considering the basic importance of nematodes in the marine ecosystem, the ‘Maturity Index’, based on the ecological characteristics and reproductive strategies of nematodes, and initially proposed for terrestrial and freshwater habitats, was then applied also to marine and brackish communities [39].

During recent years, meiofauna have been increasingly used as a collective indicator of altered functioning of marine ecosystems. Owing to their high sensitivity to several environmental perturbations, the high number of individuals (which make easier statistical analyses and reduce sampling volumes) [35], the lack of larval dispersion and the short life cycle, meiofauna are becoming a common tool with which to evaluate the ecological status of marine coastal environments [21,40]. Meiofauna have been shown to be a reliable indicator of ecological impacts on the benthic domain, not only in case of pollution [41], but also in the case of introducing ‘artificial reefs’ [42] and organic wastes resulting from mussel or fish farming activities [40,43,44].

3. Current research on Adriatic meiofauna

As in most countries, research on the marine zoobenthos in Italy has mainly focused on macrofauna. Meiofauna have been the object of scientific interest only from the 1960s, with faunistic, taxonomic and ecological studies mainly concerning the Tyrrhenian and Adriatic Seas.

3.1. *Diversity and distribution of the major meiobenthic taxa from the Adriatic Sea*

Current knowledge of the faunistic and zoogeographical status of several meiobenthic taxa is reported in the series 'Checklists of the Marine Italian Fauna' published by the Italian Society of Marine Biology (SIBM) on behalf of the Italian Ministry of the Environment, and updated in 2008 [45]. Available information on the meiofauna from the Adriatic Sea is extremely heterogeneous and most data refer to a small number of taxa, mainly from soft-bottom communities. Foraminifera, Proseriata, Gastrotricha, Nematoda, Tardigrada, Copepoda Harpacticoida are the meiobenthic groups that have been especially studied along the Adriatic coasts, either within the framework of national or international research projects (Figure 2, Tables 1 and 2).

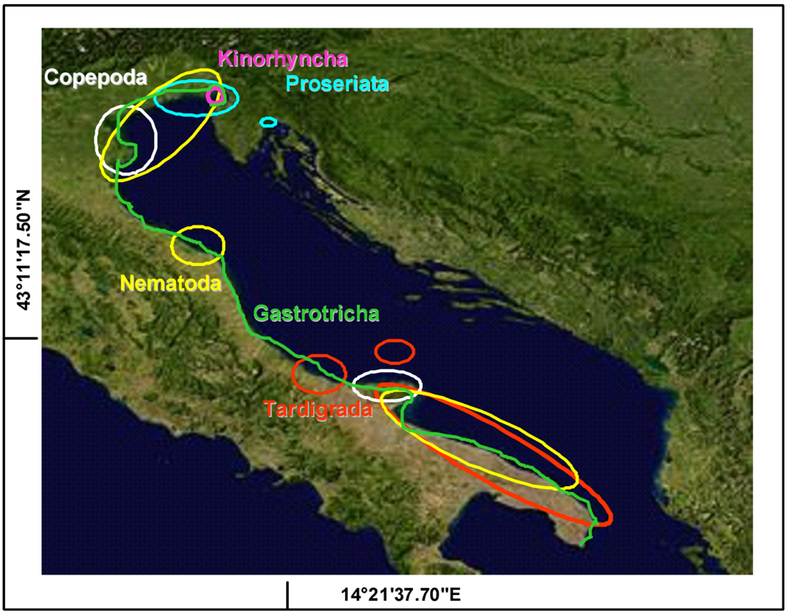

Figure 2. Adriatic areas and meiofaunal taxa which have been the object of faunistic and ecological research.

Table 1. Number of species of the major meiobenthic taxa reported from the Italian seas, from the Adriatic Sea and from its basins.

Taxon	Italian Seas	Adriatic Sea	Northern Adriatic Sea	Central Adriatic Sea	Southern Adriatic Sea
Proseriata	79	9	9	2	4
Gastrotricha	154	85	67	67	46
Nematoda	443	263	247	–	36
Kinorhyncha	48	22	21	–	1
Tardigrada	75	55	–	39	36
Harpacticoida	221	118	114	23	8

Table 2. Research projects and main scientific references on meiofauna of the Adriatic Sea.

Study focus	Adriatic Sea basin and study site	Taxa studied	Results	Research project	References
Monitoring system on meiofauna along Italian and Albanian coasts	Southern basin: Apulia coast	Total meiofauna	Higher abundances along the Italian coasts; no significant differences in diversity between the two coasts, but higher diversity at stations across the sea	INTERREG Italy–Albania 2000–2001	33, 74
Conservation and distribution of meiofauna along coasts of Apulia (Italy)	Southern basin: Apulia coast	Total meiofauna Nematoda Tardigrada	Meiofauna densities values; distribution and composition of Nematoda and Tardigrada communities	INTERREG Italy–Greece 2000–2001	
Biodiversity of meiofauna in three Italian Marine Protected Areas	Northern basin: MPA of Miramare (Trieste)	Gastrotricha Proseriata Tardigrada	Numerous new species and endemisms	BIOIMPA-PRIN 2004–2006	
Diversity and distribution of selected taxa	Northern basin central and southern basins: few sites	Foraminifera Proseriata Gastrotricha Nematoda Tardigrada Harpacticoida	Faunistic and zoogeographical status of single taxa		46–49 45, 50, 51 45, 52 45, 54 45, 55, 56 45, 57
Relations between meiofauna and habitat	Northern–central basin: Marches coast	Total meiofauna	Structure and density of meiofauna of hard and soft substrates are different	MIUR (Ministry University Research)	58
Trophic role of meiofauna	Northern–central basin: Marches coast Northern: Po River Delta	Total meiofauna Harpacticoida	Different impact of predation on meiofauna across habitats Trophic relations between Harpacticoida and gobies	MARBEF (EU Project VIFP) PRISMA2	59 63 14, 20, 60
Response of benthic Foraminifera to contaminants (trace elements)	Northern: Venice Lagoon Northern–central: Marches coast	Benthic Foraminifera	Abundance of abnormal tests in contaminated areas	ForamLag 2003–present	47, 48, 66–71
Relation between meiofaunal communities and quality of coastal water	Northern–central: Marches coast	Total meiofauna Nematoda Foraminifera	Low diversity of meiofauna, strong dominance of Nematoda, absence of Foraminifera related to polluting rivers input	CIP (Coste Italiane Protette) 2003–2005	47, 48 ,72
Effects of disturbance events on meiofaunal communities	Northern: Po River Delta, coast of Veneto	Total meiofauna Harpacticoida Gastrotricha	Recovery dynamics after disturbance events Effects of river plume Interactions between artificial reefs and soft sediments Influence of mussel farming Effects of organic pollution	MIUR (Ministry University Research) MIPAF (Ministry Agricultural Forestal Politics)	61, 62 63 42 64 65

3.1.1. *Foraminifera*

Several studies have been carried out over the last two decades on benthic Foraminifera in the Adriatic Sea [46–48]. The first and most comprehensive description of the basin-wide distribution of benthic Foraminifera in the Adriatic Sea was provided by Jorissen [46] who collected 285 samples from all over the basin, with the exception of the Yugoslavia coastal area. A total of 270 benthic foraminiferal species (including morphotypes) were documented in the basin: this diversity value can be compared with the 328 species recognised in the Mediterranean Sea [49]. Jorissen demonstrated statistically the strong influence played by oxygen concentration and food availability on the distribution and morphology of benthic Foraminifera.

3.1.2. *Proseriata*

Before the research performed within the framework of the Interuniversity Project BIOIMPA (PRIN-2004) in three Marine Protected Areas (MPAs; Porto Cesareo, Ionian Sea, Apulia, Miramare, Gulf of Trieste and Capo Caccia-Isola Piana, Sardinia), representative of the main biogeographical sectors of the Italian coasts, only nine species of Proseriata were known from the Adriatic [50]. *Inaloa cirrifera* is limited to the coastal lagoons of the upper Adriatic. The other species were all described from the eastern Adriatic: *Monocelis fuhrmanni* from the Rovinji area; *Pseudomonocelis cetinae*, only known from the mouth of the River Cetina (Croatia), and whose presence has been recently confirmed (Curini-Galletti, unpubl. data); and *Preminona insularis* from the Croatian coast. None of these species has been found elsewhere in the Mediterranean, indicating a potentially high rate of endemicity of the proseriate fauna of the basin [50]. Fifty-one species of Proseriata are currently known from the area, several of which have been described [50,51]. The vast majority of the species found (approaching 80%) are new to science. This percentage of exclusive species is among the highest known to date for the whole Mediterranean (Curini-Galletti, unpubl. data). Given the current state of our knowledge of the taxonomy and distribution of interstitial taxa, further research may prove that these supposed ‘endemism’ actually have a wider Mediterranean distribution. However, there are indeed cases of particular interest, like *Promonotus* n.sp. and *Archilina*/*Inaloa* sp. pl. *Promonotus* n.sp. was found in the Marina Julia area, occurring intertidally on *Fucus virsoides.* Characteristics of genital structures place the new species as the sister taxon of *Promonotus arcassonensis*, a species ranging in the Atlantic from the North Sea to the Gulf of Gascogne; given its peculiar niche, it is hardly to be expected elsewhere. *Archilina*/*Inaloa* sp. pl. the genus, with 10 species, 8 of which are new, resulted in the most species-rich taxon in the upper Adriatic. Apart from one species with a wide Mediterranean distribution, all the others present apomorphic features (a fission of the first chromosome pair of the set, resulting in two acrocentric pairs; a very elongate, often convoluted, copulatory cirrus) suggestive of shared ancestry. This monophyletic species-complex was widespread in the uppermost Adriatic, occurring in all habitats (brackish, intertidal to silty infralittoral sediments), and is the most outstanding feature of the Adriatic proseriate fauna (Table 2).

3.1.3. *Gastrotricha*

The Italian marine gastrotrich fauna is one of the best known in the world; to date 154 species, 91 Macrodasyida (M) and 63 Chaetonotida (C), from more than 180 localities have been identified, and an additional 25–30 species are still undescribed [45]. In the Adriatic Sea, 85 species have been recorded (50 M, 35 C) from some 60 localities. Twenty species (10 M, 10 C) are known, in Italy, only from this basin, and 12 of them (4 M, 8 C) are endemic to the Adriatic. Forty-six gastrotrich species are known from the southern basin, 67 species from the central basin and 67 from the northern basin. Although most species have a wide geographic range, including the entire basin, it is worth mentioning that 10 of 12 endemic species are in the northern Adriatic. At least two species found in northern Adriatic, *Dendrodasys ponticus* and *Turbanella* cf. *pontica* are thought to be Sarmatic elements that are tied to selected environments (i.e. brackish waters) and have been able to overcome the Messinian saline crisis [52]. Project BIOIMPA has indicated that in the northern Adriatic Sea the richest gastrotrich genera were *Tetranchyroderma* and *Chaetonotus*, followed by *Halichaetonotus* and *Aspidiophoru*s, whereas the most common genera were *Chaetonotus*, *Paraturbanella* and *Halichaetonotus*. A slight, but constant, predominance of Chaetonotida versus Macrodasyida was observed, perhaps related to the apparent preference of Chaetonotida for fine sediments. The gastrotrich diversity at the mouth of the Isonzo River is significantly high (36 species overall), one of the highest known the world over. Most species are confined to a few sites, more or less strictly estuarine, generally those along the Friuli coast: a possible adaptation of these species, in particular of *Halichaetonotus* and *Heterolepidoderma* to the estuarine/brackish environment may be hypothesised. Comparison of the data from the three investigated MPAs evidences that the north Adriatic area overall hosts a lower number of species, and also a lower average species number per station. Analyses of the taxonomic indexes suggest that the lower gastrotrich biodiversity observed is linked to the relatively reduced habitat heterogeneity of this basin rather than to its evident oceanographic confinement and also to the relatively high number of species of the genera *Tetranchyroderma*, *Chaetonotus* and *Halichaetonotus*, found exclusively in this MPA.

3.1.4. *Nematoda*

Estimates of global nematode species diversity have varied widely in the past 15 years, but it has been hypothesised that this phylum is hyperdiverse (i.e. includes more than one million of species). The marine nematodes known to date from the Italian seas count 443 species, 262 genera and 46 families. This number is comparable with that reported for the British Isles [2], and denotes a good state of knowledge if compared with that of all species reported from Europe, 1625 [53]. Information on Italian nematode fauna is mainly available from dated lists, whereas recent extensive faunistic research is very poor (see [54] for the Adriatic Sea). The Italian coast of the Adriatic has a rich nematode fauna composed of 263 species, belonging to 169 genera in 39 families. Most records concern the northern basin (247 species), whereas a lower species number has been reported from the central and southern basins [45], where 137 genera and 34 families of Nematoda along a coastal tract of Apulia (Brindisi-Gagliano) have been reported (Table 2). The genus *Theristus* (Xyalidae) was the most abundant, and was found at nearly all the stations sampled, independent of depth and sediment typology. Other genera widely represented for density and distribution were: *Epsilonema*, *Spilophorella*, *Terschellingia*, *Desmodora*, *Richtersia*, *Paramonhystera*, *Ptycholaimellus* and *Innocuonema*.

3.1.5. *Tardigrada*

Research in the Adriatic Sea has been carried out in 42 localities, and has led to the record of 55 species, five of which are new to science, two in the family Batillipedidae and three in the Stygarctidae, with two species of the latter only known from marine caves [55]. Coarser, organogenic sediment seems to host a higher number of species than finer sediment. The family Halechiniscidae appeared the most abundant and diverse, whereas in medium to fine sediments the family Batillipedidae showed the highest abundance, and Halechiniscidae showed maximum diversity. Most Adriatic species have been recorded at the Tremiti Islands, in organogenic sediment. In general, intertidal tardigrade species are fewer in number than subtidal ones. Among the most common species, *Batillipes mirus*, *B. pennaki*, *Halechiniscus remanei*, *Orzeliscus belopus* and *Echiniscoides sigismundi* are cosmopolitan species, whereas *Pseudostygarctus apuliae*, *P. rugosus* and *Parastygarctus mediterranicus* are endemic to the Adriatic Sea [45,56]. In the frame of a Project INTERREG Italy–Greece, 43 species of Tardigrada belonging to four families and nine subfamilies were recorded along the Apulian coast (Table 2). The most abundant species was *Chrisoarctus flabellatus* (Halechiniscidae), which was found at all depths and in any type of sediment, even if more often in coarse sands and at −10 m. Other species of great importance for their high abundance and wide distribution were: *Raiarctus variabilis*, *Tanarctus gracilis*, *Dipodarctus subterraneus*, *Parastigarctus sterreri* and *Actinarctus neretinus*.

3.1.6. *Copepoda Harpacticoida*

Taxonomical, faunistic and ecological investigations carried out since the early twentieth century have recorded a total of 221 harpacticoid species from the Italian marine seas. Little more than half of them (53.4%), i.e. 118 species, have been recorded in the Adriatic Sea, being evidence of an equal research effort undertaken in both the Tyrrhenian and Adriatic Seas. The 118 Adriatic species are distributed as follows: 114 species in the northern basin, 23 in the central and 8 in the southern. Moreover, almost 40 species appear to be exclusive of the Adriatic Sea: 31 of them have been found in the northern basin and only 3 and 1 in the central and southern basins, respectively. Obviously, this uneven distribution of the records does not reflect a true picture of the harpacticoid species distribution, but it is due to the higher number of studies on meiofauna carried out in the northern basin than in the others. Only five harpacticoid species, of all the above records, have proved to be endemic of the Adriatic Sea: *Psyllocamptus eridani*, *Harpacticus flexulosus*, *Pseudonychocamptus colomboi*, *Tisbe reluctans* and *T. inflatiseta*, all found in the brackish lagoons of the northern Adriatic coast. Meiofauna zoogeographical patterns remain controversial. In general, harpacticoids do not show a cosmopolitan distributional pattern, because many species seem to be restricted within well-defined zoogeographical boundaries. The relative isolation of coastal brackish-water environments could actually represent a boundary. A statistically tested comparison among harpacticoid faunal assemblages of five Italian brackish environments (three along the northern Adriatic coasts, one in the central Adriatic Sea and one in southern Sardinia) and those of five Ponto-Mediterranean lagoons (two from French coast and one from Tunisia, Sinai and Danube River Delta, respectively) was carried out [57]. It revealed the four harpacticoid assemblages of the Adriatic lagoons to be more related to that of the Pontic lagoon than to those of the western Mediterranean brackish environments, Sardinia included. That affinity appeared to be mainly due to the sharing of a little group of species with an exclusive eastern Mediterranean and Ponto-Caspian (Sarmatic) distribution, and it is supposed to date back to the late Quaternary eustatic events.

A large area of the southern Adriatic Continental Shelf between Italy and Albania was investigated. Results showed significant differences in total meiofaunal densities at the different coastal sites. Significantly higher meiofaunal abundances were recorded along the Italian coast [(average ± SD) $369 \pm 340\,\mathrm{ind} \cdot 10\,\mathrm{cm}^{-2}$] compared with the Albanian coast, ($211 \pm 283\,\mathrm{ind} \cdot 10\,\mathrm{cm}^{-2}$). By contrast, no significant difference in meiofaunal diversity was detected between the two coasts. Both Italian and Albanian stations showed similar taxa composition, with nematodes representing in all cases the dominant group accounting on average for the 85% of the total density.

3.2. *Ecological research on the Adriatic meiofauna*

Handling meiofauna presents some technical problems related to the microscopic size of these organisms, and a certain low-level identification can be difficult in absence of specific identification keys because of the need to check fine diagnostic details of the anatomy. These are the reasons why most recent and current studies on Adriatic meiofauna have focused on the ecological aspects, mainly their relations with the habitat, their trophic role in the marine ecosystems and the reactions of meiofaunal organisms to environmental changes, both natural and anthropogenic.

3.2.1. *Relations between meiofauna and habitat*

Although most studies dealing with meiofauna have been carried out on soft bottoms, a recent study [58] report that meiofauna of hard and soft substrates display significant differences both in terms of density and assemblage structure. Meiofauna from rocky substrates were dominated by crustaceans (copepods, nauplii and amphipods) while soft sediments were largely dominated by nematodes (∼90%). Significant temporal changes of meiofaunal density were observed on both hard and soft substrates, with higher densities in spring to summer and lowest abundance in winter. The nature of the substrate (hard vs. soft) is one of the main factors responsible for the differences observed between hard- and soft-bottom meiofauna assemblages, whereas phytal coverage and substrate complexity influences the structure of hard bottom assemblages.

3.2.2. *Population dynamics and trophic role of meiofauna*

Meiofauna have been increasingly used as a model for investigating the role and strengthen of biotic interactions in either soft and hard substrata. For example, the effects of epibenthic predation on metazoan meiofaunal assemblage on soft and rocky substrates were compared by means of experimental exclusion of potential predators [59]. Different patterns of abundance were observed in uncaged versus caged plots, across habitats: in caged soft substrates, the abundance of nematodes, copepods, polychaetes and the number of meiofaunal taxa increased, whereas the exclusion of predators from rocky substrates showed less clear patterns. The different impact of predation across habitats may be explained in terms of differences of spatial variability and substrate complexity.

It is very useful to know the life-history traits of meiofaunal organisms to understand their ecological role in the benthic ecosystem. This may be achieved by studying population dynamic parameters of species directly in the field where populations are fully experiencing biotic interactions. Yearly trends in field population dynamics of the most abundant harpacticoid species in a brackish water environment of the Po River Delta have been investigated [60]. Parameters such as total abundance, development stages, sex ratio, egg clutch and brood sizes were directly measured in order to estimate birth and death rates and *per capita* rates of change using a modified version of Edmonson’s egg-ratio method. The study revealed, among other results, that the dominant species, *Canuella perplexa*, started reproducing at the end of March and stopped at the onset of autumn. Its protracted summer breeding season reflects its ability to utilise a wider spectrum of food resources. *C. perplexa* populations showed a density peak in early summer but during August–September, despite its maximum percentage of ovigerous females bearing, on average, >80 eggs per egg sac (an unusual figure for harpacticoids), the population density of this species decreased sharply owing to the strong predatory pressure of gobies. Indeed, the gut contents of juvenile marbled gobies, *Pomatoschistus marmoratus*, was contemporarily investigated in the same lagoon during summer–autumn months of the same year [20]. Thanks to the energetic and productivity data already known for *C. perplexa* in the same environment [14] and to the equations for metabolic rates of teleosts from literature, it was possible to estimate the impact of predation by gobies on this prey species. In August, predation was totally centred on adult copepods which were present in very large numbers in all predator gut contents. The energy supplied by specimens of *C. perplexa* was high enough to sustain, almost alone, the gobies’ daily energy requirement.

The situation changed in September, when the adult copepod population declined dramatically and gobies shifted their predation pressure to the less energy-providing copepodites, while at the same time widening their prey spectrum. Considering that *C. perplexa* increased its breeding effort during that month, the question remains whether gobies preyed preferably on populations of this species because of its summer increase or the harpacticoid enhanced its reproductive effort to cope with such a heavy predation pressure.

3.2.3. *Meiofauna as a bioindicator: case studies applied in the Adriatic Sea*

Numerous studies dealing with total meiofauna or single meiobenthic taxa as a tool for evaluating environmental alterations have been carried out in the Adriatic Sea in recent years. Some of them are part of wider national or international applied research projects.

Meiofaunal community composition is diversely altered by disturbance events. Its subsequent restoration, when it occurs, depends on the different spatial scales and develops according to the different taxa which are involved. Thus, it is useful to know the dynamics of these processes to better evaluate the altered status of an impacted environment. A re-colonisation experiment of artificially defaunated sandy sediments has been carried out in a lagoon of the Po Delta (Sacca di Goro) in order to describe the recovery dynamics of meiobenthic communities after a mimicked small- and large-scale disturbance [61]. Colonisation patterns in relation to the distance from the source of colonisers seem to differ according to whether the dispersal mode of the organisms of different taxa is a passive process or an active migration.

In the shallow water, eutrophicated lagoons of the northern Adriatic coast, such as the Valli di Comacchio, heavy oxygen depletion of the entire water column occurs as a consequence of summer dystrophic crises. In order to investigate the recovery dynamics of meiofauna communities both in the phytal habitat (*Ruppia* sp.) and in the unvegetated muddy sediments after an induced hypoxic/anoxic disturbance, a field experiment was carried out by incubating portions of those habitats with dark/light/no benthic chambers for three days [62]. Nematodes showed a better resistance to short-term anoxia than copepods. Nematode communities exhibited a slower recovery, and the colonisation rates differed depending on the trophic habitus of the species. By contrast, copepod communities appeared to be remarkably resilient in both habitats thanks to the higher dispersal capability of their species.

The effects of the Po River plume on the abundance of meiofauna in coastal sediments of the north-western Adriatic Sea were investigated [63]. The plume inputs and frontal systems, enhancing phytodetritus accumulation and benthic prokaryote response, may influence abundance, taxa richness and composition of the meiofaunal assemblages. Also the interaction between artificial reefs and surrounding soft sediments, independent of differences in latitude, sediment texture and trophic conditions, can alter the composition of meiofaunal assemblages, with potentially important implications for their role in secondary production and energy transfer to higher trophic levels [42]. Meiofauna have also been demonstrated to be sensitive to organic wastes from mussel farming, which, however, did not exert significant changes in abundance or taxonomic richness [64]. Severe changes in gastrotrich communities consequent to the presence of organic pollution along the northern Adriatic coast were recorded [65].

The use of benthic Foraminifera as bio-indicators of environmental quality may concern population density and diversity, assemblage structure, reproduction capability, test morphology including size (dwarfism), prolocular morphology, ultrastructure, pyritisation, abnormality, and chemistry of the test [66,67]. In some modern assemblages, abnormal tests have been reported in areas contaminated by trace elements, domestic sewage, and various chemicals, including liquid hydrocarbons (for a review see [66,68]). In the last few years many studies on benthic Foraminiferal assemblages have been carried out in different parts of the world in areas exposed to different kinds of marine pollution [48,69–71]. The first Italian data concerned the Goro lagoon [69], where the occurrence of a high percentage of abnormal tests (up to 10% of the whole assemblage) corresponded to sites where higher trace element concentrations were prevalent. Project ForamLag (2003) was set up with the aim of studying the response of benthic foraminifers to contaminants such as trace elements in lagoons, wetlands and salt marshes along the Italian coasts, and of evaluating their role in biomonitoring. Transitional environments investigated include the lagoons of Venice [70] and Santa Gilla [71]. The relations between living benthic Foraminifera and trace element content have been documented in the shelf area of the central-western Adriatic Sea. The Foraminiferal Abnormality Index (FAI) and the Foraminiferal Monitoring Index have been proposed [47] to quantify and compare the percentages of abnormal specimens and species, respectively. A statistical approach of these data was used for a possible control of the pollutants both on the taxonomic composition within the assemblages and the development of test abnormalities [48]. Results confirmed that *Ammonia parkinsoniana* is a very sensitive and intolerant species to trace element pollution since it prefers clean to low polluted environments.

Higher trace element concentrations lead to an overall increase in abundances of species *Ammonia tepida*, *Aubignyna perlucida*, *Eggerelloides scaber* and *Nonionella turgida*, which, therefore, may be considered as tolerant species.

A detailed picture of the quality state of the Marches coasts was the object of the Research Project ‘Coste Italiane Protette’ (CIP) which was carried out using a multidisciplinary approach [47]. Meiofaunal assemblage showed an especially low diversity, and a very strong dominance of nematodes was generally recorded (Semprucci, unpubl. data). The significant decrease in sensitive meiofaunal taxa and the almost total absence of Foraminifera near the coastline appeared to be related to a greater anthropic disturbance mainly due to the influence of the Foglia and Metauro rivers, but also of a minor stream Arzilla [47,72].

Meiofaunal abundance and diversity have been used in a network analysis approach to evaluate the health of the southern Adriatic benthic system. Among network indicators, ascendency values (here intended as a proxy of benthic system functionality and efficiency) showed a different spatial pattern between the southern part of the Italian coast and the Albanian and northern Italian coasts, with significantly lower values found in the latter. Along the Albanian coast, ascendency displayed peak values in coastal stations close to river outlets, whereas along the Italian coast, higher values were related to the presence of human and industrial activities [33]. Even if increases in ascendency are generally reported to be related to an increase in maturity of the systems [73], previous observations on the micro- and meiobenthic subsystems [74] showed the increase in ascendency as a function of an increase in the microbenthic loop subsystem activity, devoted first to the assimilation and later to the dissipation of the increased organic matter and nutrients in the system.

Based on these findings, the most efficient trophic networks and the most complex cycling structures were found in deeper and more oligotrophic areas and in shallow areas characterised by lower organic loads and anthropogenic pressure. By contrast, in areas subject to greater anthropogenic action, the micro- and meiobenthic loop sub-systems showed clear dissipative behaviour with highly active networks but low efficiency of resources exploitation.

4. Future perspectives in the research on Adriatic meiofauna

The future of research on Adriatic meiofauna sees the continuation and the development of studies along the two main lines of interest currently followed by all the research groups working on meiofauna: biodiversity and ecology.

The assessment of the biodiversity of this rich and heterogeneous assemblage is little more than at the beginning, considering that current knowledge concerns only some of the numerous meiobenthic taxa. Widening of the research to still little known taxa, as well as to areas and habitats not yet explored, appears of great importance for outlining a more detailed picture of the composition and distribution of the various meiobenthic groups in the Adriatic Sea. Faunistic investigations will allow compilation or integration of the already existing checklists and computerised databases which can be related to regional and global networks to world research benefit. Molecular and genetic studies will probably be of increasing weight for assessing the distribution and the evolution of taxa, as well as of their phylogenetic relations.

A further impulse to faunistic research is essential not only to improve general knowledge of the Adriatic fauna, but also to give a solid base of data which is necessary for the ecological and applied investigations. For this reason, specialists of the single taxa should make an effort to produce identification keys which could be widely used, even by nonspecialists. Knowing and monitoring the faunistic situation over time is also of great importance for planning conservation actions, which now appear to be more urgent than in the past, in particular in the coastal protected areas. For example, as reported above, available information points to a particular interest of the proseriate fauna in the upper Adriatic. The issue of conservation of this apparently unique 'sub-Atlantic pocket', in the face of present warming trend may thus be raised. Within this context, the education and training of young researchers in the taxonomy and faunistics of meiobenthic taxa appears of basic importance for ecological and applied studies, which certainly will continue to form the bulk of research on meiofauna. The study of their relations with habitat complexity, analysis of the effects on meiobenthic diversity and distribution of disturbance factors of different natures, and possible ways of using this fauna for impact assessments will certainly be primary goals of the research on meiofauna of Adriatic as well as on that of other seas. Prerequisite for aiming at these perspectives are the effective collaboration among meiobenthologists and their close interactions with other benthologists, also through international protocols and research programmes. The set up of a standardised protocol for the joint study of macrofauna and meiofauna is an achievable goal, which would greatly improve and speed up information on the status of zoobenthic communities, so favouring the planning of actions of conservation or restoration of the marine habitats.

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